NEW YORK ENTOMOLOGICAL SOCIETY
LXXXIX(1), 1981, pp. 43–52

NOTES ON THE BIOLOGY OF A COMMON SUNFLOWER BEE, *MELISSODES (EUMELISSODES) AGILIS* CRESSON

F. D. Parker, V. J. Tepedino and G. E. Bohart

Abstract.—Melissodes agilis, an anthophorid bee that is oligolectic on sunflowers, was found nesting in and adjacent to a planting of commercial sunflowers in northern Utah. Observations and excavation of nests yielded information on nest architecture, larval morphology, foraging activity, and parasites. The species will probably be most valuable as a commercial pollinator where minimum- or no-tillage agricultural practices are appropriate.

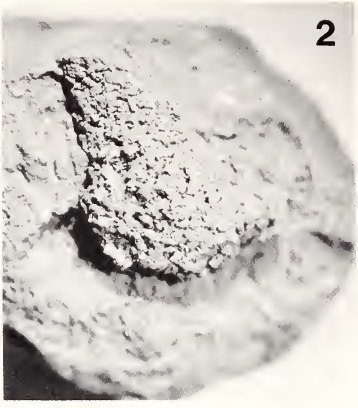
Introduction

The commonest native bee species frequenting sunflower (*Helianthus* spp.) in the western United States is *Melissodes agilis* Cresson, a ground-nesting member of the Anthophoridae. Although *M. agilis* is probably responsible for a significant proportion of sunflower pollination throughout the west (Parker 1981a, b), biological information on this commerically important species is limited to a brief note on the nest tumulus and length of the main burrow (Rau 1922) and a comment by Custer (1928) that a female *Melissodes* (presumed to be *M. agilis*) entered a nest of *Svastra obliqua* (Say), another anthophorid bee. During the summer of 1979, large numbers of *M. agilis* were observed visiting and nesting in our plantings of commercial sunflowers in northern Utah; and we took the opportunity to study the biology of this species. Specifically, we provide information on nest architecture, larval morphology, nest associates, seasonal occurrence, foraging activities, and sleeping aggregations of males.

Nesting Site

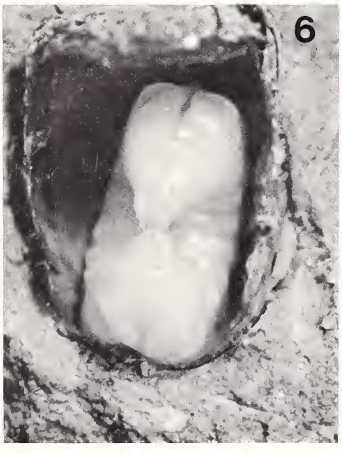
Melissodes agilis nested in and between irrigation furrows in a 1-acre (0.4047-ha) plot planted to sunflowers (*Helianthus annuus* variety *macrocarpus* (D.C.)) and summer squash (*Cucurbita pepo* L.) near Logan, Utah, during July and August 1979. The site was nearly flat and the soil type was Millville Silt loam. More than 20 nests of *M. agilis* were marked with stakes and some were excavated in September. The nests appeared randomly distributed throughout the sunflower and zucchini plots; a few were as close together as 12 cm. The following description of the nests was taken from 6 excavated nests with cells.


1


2


4


5


6


7

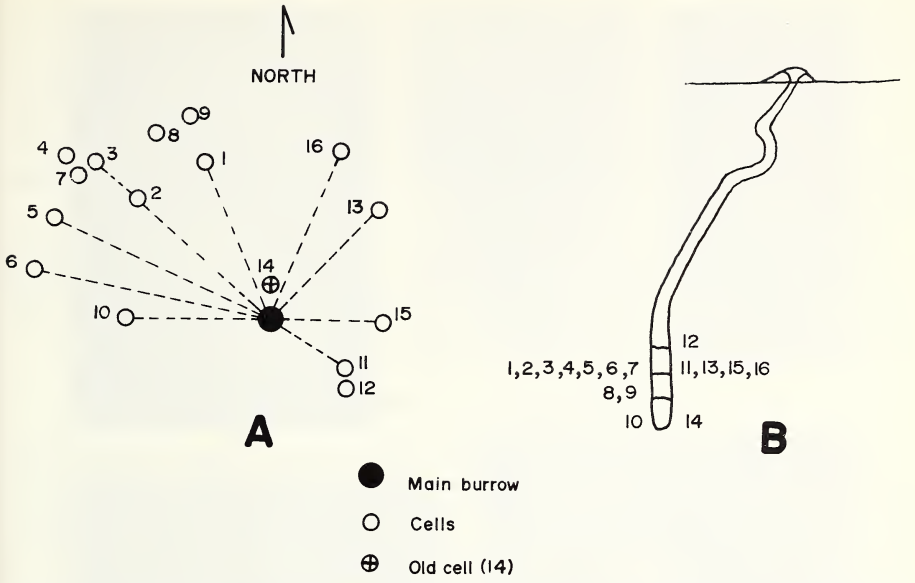


Fig. 3. Diagram of typical *Melissodes* nest. A. Arrangement of cells. B. Cross section of nest with depth of cells indicated.

Nest Architecture

No bees were observed initiating nest excavation; nests were located by observing bees entering or leaving their nests or by observing the newly excavated crater-like tumuli. The mound of soil from a typical nest excavation measured 5 cm across and 1.5 cm high. However, tumuli were not always evident. The entrance hole was in the middle of the crater and averaged 7 mm in diameter (Fig. 1). The entrance hole was not plugged during nest provisioning.

When we excavated the nests, the main and lateral burrows were filled with soil, but the main burrow could be traced by blowing out the soil and refilling it with plaster of Paris powder. Typically, the main burrow was 7 mm in diameter and spiraled downward for 4 cm before descending nearly vertically to a depth of about 12 cm (range 11–17 cm), where the first cell was placed. The main burrow was unlined, but the walls were smooth. It

←

Figs. 1, 2, 4–6. 1. Nest entrance and tumulus of *Melissodes*. 2. Compacted soil in filled *Melissodes* burrow. 4. Waxed lined cell of *Melissodes*. 5. Tops of 2 *Melissodes* cells exposed during nest excavation. 6. Overwintering *Melissodes* larva in cell; cocoon cut away to expose layers of the cocoon.

was not possible to trace the route of the lateral branches because they were filled with tightly packed soil (Fig. 2). Lateral burrows were from 1 to 10 cm in length and radiated away from the main burrow (Fig. 3). In one nest, the cells were distributed in a pattern indicating that at least 12 lateral burrows diverged from the central main burrow. Since the cells were found at 8 levels (Fig. 3), it appeared that most of the laterals were begun at different levels.

The number of cells/nest ranged from 1 to 27 ($\bar{x}$ = 11.5). Cells were found at depths ranging from 11 to 19 cm below the soil surface. In multi-celled nests, some cells were about 1 cm below an adjacent one, an indication that some lateral burrows contained more than one cell.

Cell Structure and Morphology

The oval cells were vertical in orientation. Each cell was 7–8 mm wide at its greatest diameter and 8–14 mm long (Fig. 4). Cell walls were made by the bee compacting about 2 mm of soil against the "roughed-out" original excavations. Following this, the inner walls (Except the cell cap) were coated with wax. The wax lining was evenly applied to all cell walls and was thick enough to be readily scraped off with an insect pin. The upper ⅓ of each cell was paler and slightly rougher than the basal portion. The area of overlap between these color bands was darkened. The cell cap was composed of rings of soil, but the precise pattern could not be determined since the top of every cell was at least partially destroyed during excavation. In all cells examined, the pollen provisions had been consumed.

Most fecal material was incorporated into the cocoon layers, but at the top of the cell were some loose, concentric, tubular strands of fecal pellets in a 3 mm thick layer (Fig. 5). The larva started the cocoon by first lining the cell walls (except the top) with a thin varnish of silk. Over this layer it smeared successive, longitudinally directed strands of yellowish fecal material, separated but held together by layers of silk. Inside the fecal layer the larva produced a shiny inner cocoon of thin, transparent, yellowish silk (Fig. 6), in which it embedded a network of larger, darker strands. This inner envelope was entire and of uniform thickness and its inner surface was smooth and shiny. It was surmounted by a dome-shaped cap composed of several sheets of silk loosely held together.

The overwintering prepupal larvae were creamy white and rather flaccid.

→

Figs. 7–14. 7–8. Overwintering *Melissodes* larvae. 7. Lateral view. 8. Larvae tilted to illustrate lateral lobes. 9–10. *Triepeolus* prepupae. 9. Ventral view. Note head capsule of 1st instar larva (arrow). 10. Lateral view. 11–12. Cells with *Triepeolus*. 11. Basal ring (arrow) that holds prepupa. 12. Prepupa surrounded by fecal pellets. 13. Puncture in cell wall made by *Triepeolus*. 14. Egg chamber of *Triepeolus*. Note shriveled egg chorion.

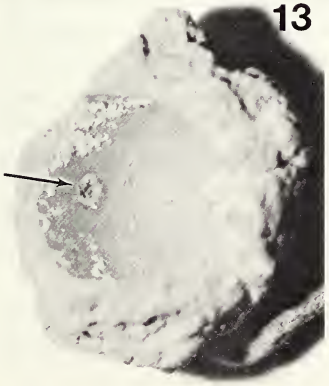

8

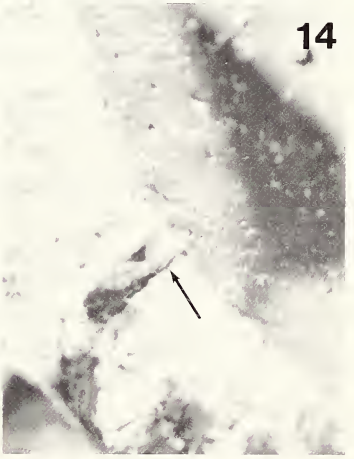

9


10


11


12


13


14

They were C-shaped and vertical with their weight resting on the posterodorsal area (Figs. 7, 8).

Nest Associates

Three nests contained a total of 7 cells parasitized by the cuckoo bee *Triepeolus helianthi* (Robertson). The distinctive rigid prepupae (Figs. 9, 10) were held erect in the center of the cell by a basal ring of feces or pollen (Figs. 11, 12). The tubular-shaped fecal pellets were yellowish and were deposited in short strands, but in layers, on the upper ⅔ of the walls and beneath the cell cap. The egg chamber (0.5 mm wide and 2 mm long) was located 40% of the way up the side wall and perpendicular to the cell walls (Figs. 13, 14). There was no evidence that the larvae deposited any silk. Hurd and Linsley (1959) reported that adults of *T. helianthi* entered nests of *Melissodes composita* Tucker, but they did not find any parasitized host cells.

One cell contained the coarctate prepupal larva of the meloid beetle *Nemognatha*. Another two *Melissodes* cells contained castings of earthworms, which presumably were deposited in the cell before the bee larvae matured.

Observations of Adults

Seasonal occurrence.—Since sunflowers were planted at three different times, bloom was available for the entire season. We counted all bees on the flower heads at 0900, 1100, 1300 hr every Monday, Wednesday and Friday from 25 July to 4 September. Both male and female *M. agilis* were present on July 25 when bloom began. At this time their wing margins were entire and their body hairs were not worn, indicating recent emergence. Both sexes were abundant throughout the summer. The pattern of their seasonal occurence suggests a single generation/year. Their abundance from week to week closely followed the abundance of sunflower bloom (Fig. 15).

Daily activities.—Males were recorded more frequently from flower heads than females (2.4♂/1.0♀). Initially, males were more abundant at 0900 hr than at any other time, but in late August and early September, when morning temperatures began to be quite cool, their abundance was similar in all count periods.

Males gathered on sunflower heads in sleeping aggregations of from 2 to 20 bees/head in late afternoon and during inclement weather. No observations were made to determine if they chose the same sleeping cluster or the same flower head each night. They clustered in partially opened heads under the large ray petals. (The heads had to be tilted back before the bees could be seen.)

Female *Melissodes* were most abundant on the flowers early in the day. For example, at 0900 hr twice as many females were present as at 1100 hr,

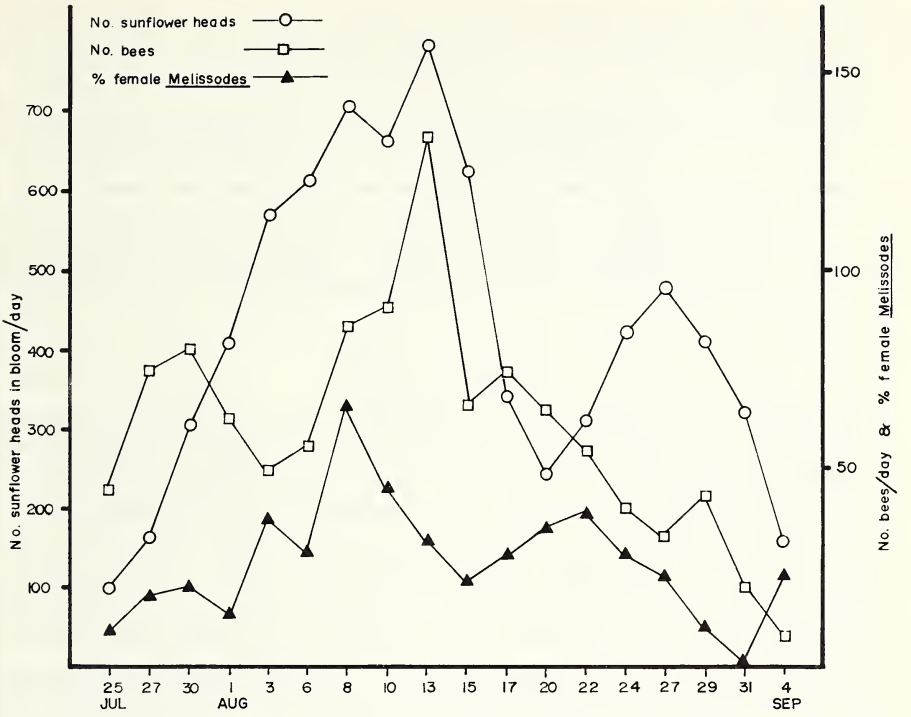


Fig. 15. Seasonal abundance of sunflower heads in bloom, number of *Melissodes*, and percentage of female *Melissodes*.

and at 1300 hr, about ⅓ as many females were present as at 1100 hr. Apparently, most of the females remained in their nests in the afternoon; this was corroborated by observations of the activity of individual females at their nests (see below). Female *M. agilis* provisioned their nests exclusively with sunflower pollen. The maximum pollen load carried by a female bee was estimated at 330,000 grains (estimated by washing the pollen from the body hairs and counting the pollen grains with a haemocytometer) (Parker 1981b).

Triepeolus helianthi was present throughout the observation period. The activity pattern of this cuckoo bee varied with the time of day. In the morning, females were often observed flying slowly several inches above the soil and investigating all types of holes. Several were seen entering *Melissodes* nests where they remained only a few minutes (see below). In the afternoon, *Triepeolus* spent more time on the flowers than in the morning. Their abundance on flower heads at 1300 hr was nearly double that at 0900 hr. Thus, this parasite appears to search for and invade host nests primarily in the morning when most host adults are foraging and to forage in the afternoon when *Melissodes* remain in their nests.

Table 1. Mean time of foraging trips and within-nest periods of two *Melissodes agilis* females on three observation dates. Initial foraging trips for each day and extended within-nest periods (4, see text) excluded. Numbers in parentheses are standard deviation and sample size, respectively.

Observation date (August)	Mean time/foraging trip (sec)		Mean time within nest (sec)	
	S	M	S	M
2	231.5 (±306.5; 10)	293.8 (±225.6; 9)	43.3 (±13.0; 9)	57.8 (±11.8; 8)
7	501.1 (±360.6; 11)	594.3 (±408.1; 9)	65.6 (±15.6; 10)	99.6 (±83.5; 9)
13	950.5 (±969.5; 11)	1,086.8 (±715.0; 9)	84.8 (±28.0; 11)	112.3 (±90.3; 8)

Foraging Activity

We monitored the activity of two female *Melissodes* bees at the nesting site on three mornings, beginning at 0600 hr and using a stopwatch and portable tape recorder. The nests were within 50 cm of each other near the top of a furrow that separated a row of zucchini from the periphery of the planting. We recorded times for commencement of activity and the number and duration of trips from the nest as well as periods spent within the nest.

Both nests were unplugged and were without tumuli each morning when observations began. Bee activity commenced between 0630 and 0745 hr. Activity began earlier when temperatures were warm and cloud cover slight. Bee S always became active first and made her initial trips from the nest 5–15 minutes before bee M. The first trip was invariably an extended one for both bees; it varied from 21 to 32 minutes in duration. Most other trips were of shorter duration (Table 1). Bees returning from short trips invariably carried pollen. Bee S also consistently completed her foraging trips more rapidly than did bee M. Bees entered their respective nests from return flights without hesitation and never investigated each others' nests.

There was no discernible difference between the duration of early and later foraging trips for either bee on any date, as might be expected if pollen or nectar were becoming limiting later in the morning. However, foraging trips became longer as the month progressed for both bees. The relatively extended trips of 13 August were associated with sporadic rainfall and heavy cloud cover throughout the morning. Both bees were trapped in the field by rain on several occasions and did not return until the rain had ceased. Although cloud cover remained heavy, both bees left for additional foraging trips after brief periods in the nest.

Periods spent within the nest after the bees returned from foraging trips were usually short (30–150 sec); presumably the pollen and nectar that the bees had collected were deposited during these brief periods in the nest. Occasionally, within-nest periods were much longer; four such periods ranging from 21 to 41 minutes were recorded. We believe that pollen loaf prep-

aration, egg laying and cell closure occurred during these extended within-nest periods. If this is so, then the number of foraging trips necessary to provision a single cell can be estimated from the ratio of short/long within-nest periods. For the two bees, we recorded 55 short and 4 long periods, for an estimate of approximately 14 foraging trips/cell.

On the first two dates, we terminated observations at 1000 hr, when the bees had been in their nests for at least 30 consecutive minutes. Foraging appeared to cease on both days by approximately 0915 hr. By this time, bee S had made 11 trips on 2 August and 12 on 7 August; bee M had made 10 trips on each day. Subsequent foraging activity was minimal, as previously shown by comparisons of numbers of females recorded on flowers at the different time periods. An exception was on 13 August, when the bees foraged in sporadic rain until just after 1100 hr. Although we continued observations until 1200 hr, neither bee emerged again. It is interesting to note that at 1100 hr, bee S returned from her 12th trip and M returned from her 10th trip, the same number as had been made on previous days.

We observed a single intrusion by *Triepeolus helianthi* into the nest of bee S on 2 August. The cuckoo bee was first seen flying around the nesting site at 0755 hr, while both *Melissodes* were active. The *Triepeolus* remained in the vicinity resting on the ground or on nearby vegetation. At 0803 hr, she briefly investigated the entrance of S's nest while the latter was out and then moved to about 10 cm west of the entrance. S returned, remained in the nest for a brief period, and left at 0807 hr. As S was leaving, *Triepeolus* began to move towards the entrance and entered less than one second after S had left. *Triepeolus* remained in the nest for 90 sec, then crawled out and down the furrow. She then flew to a nearby grass blade, where she remained, pulsated her abdomen for several seconds and then left. When the nest was excavated in September, two larvae of *Triepeolus* were found.

Discussion

This study and those of Parker (1981a, b) have shown that *Melissodes agilis* possesses numerous characteristics which make it a valuable pollinator in commercial sunflower plantings. The emergence of *M. agilis* adults was closely synchronized with the initiation of sunflower bloom, and numbers of bees followed the number of flowers available (Fig. 15). Females exclusively used sunflower pollen to provision their cells (Parker 1981b). In contrast to some other species of anthophorid bees in which the nesting site is patrolled by males in their search for females (e.g. *Centris,* Alcock et al. 1977), male *M. agilis* patrol the flowers for prospective mates. Thus, both sexes are important pollinators. Finally, because females nested in or adjacent to the planting, foraging trips were of short duration, and females were probably able to complete approximately 1 cell/day. Elsewhere (Parker

1981a, b) has shown that *M. agilis* is also a more efficient pollinator than the commonly used honey bee. Indeed, although the honey bee is usually credited for most sunflower pollination (McGregor 1976), natural field populations of *M. agilis,* which are usually ignored, may be more important.

The tendency of *M. agilis* to nest in sunflower fields makes their populations vulnerable to certain tillage practices. Since cells were constructed at soil depths between 11 and 19 cm, tillage practices that disrupt the soil below 10 cm are likely to have a devastating effect on populations of *M. agilis*. A zero or minimum tillage system (Robinson 1978), where appropriate, would be least hazardous to *Melissodes* populations.

Acknowledgments

Appreciation is extended to our technichians, D. Veirs, C. Hatley, and K. Ruggeri and part-time help G. Trostle and J. Higginson, for their assistance in conducting field work and nest excavations. Thanks are also due to E. Gorton Linsley, Univ. California–Berkeley and W. E. LaBerge, Illinois Natural History Survey, for reviewing the manuscript.

Literature Cited

Alcock, J., C. E. Jones and S. L. Buchmann. 1977. Male mating strategies in the bee *Centris pallida* Fox (Hymenoptera: Anthophoridae). Am. Nat. 111:145–155.

Custer, C. P. 1928. On the nesting habits of *Melissodes* Latr. Can. Entomol. 60:28–31.

Hurd, P. D., Jr. 1979. Apoidea, p. 1741–2209. *In*: Catalog of Hymenoptera in America North of Mexico. Vol. 2. K. V. Krombein, P. D. Hurd, Jr., D. P. Smith and B. D. Burks (eds.). Smithsonian Institution Press, Washington, D.C.

——— and E. G. Linsley. 1959. Observations on the nest-site behavior of *Melissodes composita* Tucker and its parasites, with notes on the communal use of nest entrances. Entomol. News 70:141–146.

McGregor, S. E. 1976. Insect pollination of cultivated crop plants. U.S. Dep. Agric., Agric. Res. Serv. Agric. Hdbk. No. 496, Washington, D.C.

Parker, F. D. 1981a. Sunflower pollination: abundance, diversity, and seasonality of bees and their effect on yields. J. Apic. Res. (In press).

———. 1981b. How efficient are bees in pollinating sunflowers? J. Kans. Entomol. Soc. (In press).

Rau, P. 1922. Ecological and behavioral notes on Missouri insects. Trans. Acad. Sci. St. Louis 24:1–71.

Robinson, R. G. 1978. Production and culture, p. 89–143. *In*: Sunflower Science and Technology, J. F. Carter (ed.). Amer. Soc. Agron., Madison, Wisc.

Bee Biology and Systematics Laboratory, Agricultural Research Science and Education Admin., USDA, Utah State University, UMC 53, Logan, Utah 84322.

Received for publication October 30, 1980.